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A preliminary study into the use of canopy invertebrates and sampling techniques in relation to forest indicators in a fragmented Scottish woodland – application and management

Natalie Walsh

Project Advisor: [Stephen Burchett](#), School of Biomedical and Biological sciences, Plymouth University, Drake Circus, Plymouth, PL4 8AA

Abstract

Caledonian forests within the Scottish Highlands have experienced severe fragmentation and currently remain as small isolated habitats. Canopy invertebrates within these forests play an important role in ecosystem functioning and may be potentially used as forest indicators for the use in forest management. Four different low-cost invertebrate trapping methods were deployed into birch, oak and Scots pine trees, comparing family diversity and composition between tree and trap types. Data on canopy spread, tree height and d.b.h were also tested to see if they influenced family composition of invertebrates. Collected data found little difference in family diversity and composition between tree types. However, trapping methods were shown to be effective in demonstrating taxa relation to trapping method, being highly taxa specific. Fan traps were found to predominantly catch Diptera families, whilst thrashing and bark-traps showed to be more specific to non-flying invertebrates, families using the tree substrate for dispersal. Canopy spread was unable to explain most family composition found between tree or trap types, indicating that other environmental parameters are likely to have a stronger influence on family composition. Climatic conditions, in particular seasonality, are likely to have been one of the strongest influences on this study. This signified that the majority of invertebrates collected were likely to be permanent year-round residents and consequently inadequate representatives of family diversity within the tree types. This study was a preliminary investigation into testing invertebrate trapping methods within trees, and has the potential to be applied in the future to fragmented and regeneration areas to indicate forest health, deterioration or regeneration. This study should be long-term and be extended over a minimum time period of five years, including seasonal sampling.

Introduction

Since Neolithic times (~8,000 years ago) temperate forests have experienced severe anthropogenic disturbances such as exploitation, insufficient management and economic pressures, reducing them to fragmented 'habitat islands' (Christie et al. 2009; Foley et al. 2005; Ozanne et al. 2000; Peterken, 1977). In addition, more recent levels of anthropogenic habitat degradation have been seen as a major driver in the exacerbation of global climate change, through the emission of greenhouse gases and the destruction of important carbon stores (i.e. trees) (Dixon et al. 1994).

The UK currently remains one of the least wooded regions in Europe, with a remaining 12% of terrestrial land covered in forest (Sumnall et al. 2011). Here the Scottish Highlands are home to the characteristic native Caledonian forest, recognised as an important habitat under the EU habitats directive (Davies, 2011). They are characterised by stands of Scots pine (*Pinus sylvestris* L.), often mixed with birch (*Betula* spp. L.) on western sites and occasionally oaks (*Quercus* spp. L.) in more southerly locations (Davies, 2011; Summer et al. 1999). The Caledonians support rare and indicative species of ancient woodlands contributing to their conservation value, including the capercaillie (*Tetrao urogallus* L.), red squirrel (*Sciurus vulgaris* L.) and the Scottish crossbill (*Loxia scotcia*), Scotland's only endemic species (MacMillan et al. 1998; Summer et al. 1999). Historically, these pinewoods covered around 1.5 million hectares of Scotland, but have experienced severe habitat degradation and fragmentation throughout (Baines et al. 1994; Robbins and Fraser, 2003). Most of these changes occurred between the 17th and 19th centuries from agricultural development and the expansion of the commercial timber industry. More recently commercial plantation schemes initiated by the Forestry Commission (FC) further affected these forests. For example, during the 20th century FC adjusted its afforestation schemes, increasing land cover in the Highlands 3-fold of that present in the 1920's (Mather, 2004). This turnaround has been recognised as the 'Forest Transition Theory' – the changeover of an area from a net forest loss to net forest gain over a period of time. Ironically, most areas were replanted with non-native species such as sitka spruce (*Picea sitchensis* (Bong.) Carr.) rather than native species. This economically important species boosted the productivity and economy in the area, but caused detrimental impacts to the areas ecosystem services. As a consequence, native forests remain sparse and are instead replaced by stands of monocultured trees, with more than half of them being less than 30 of age (Baines et al. 1994; Mather, 2004; Robbins and Fraser, 2003).

Canopy invertebrates within temperate forests have been largely understudied with more efforts being focused to tropical regions (Stork, 2008). They are thought to be the most diverse and species rich fauna on the planet, playing major roles in the maintenance and functioning of ecosystems (Wilson, 1987). They are important contributors to the ecosystem as a direct food source, influencing trophic and predator-prey interactions, pollination, seed dispersal and herbivory and so affecting nutrient and mineral cycling (Lowman & Wittman, 1996; Rinker & Lowman, 2004). Erwin (1982) originally estimated the global arthropod species number to 30 million based on beetle sampling in Neotropical trees (*Luehea seemannii*). However, more recent studies have revised this figure to 5-10 million species. This discrepancy in species number was accredited to the unrealistic extrapolation of Erwin's data. Erwin used the richness and host specificity data of beetles derived from only one tree species, which was thought to be a naive estimate (Odegaard, 2000). Invertebrates

are thought to be so numerous due to their ability to adapt to almost every available niche within a tree, enabled by the extremely diverse range of life history strategies demonstrated between species (Basset, 2001). Moreover, their distribution within forests are strongly influenced by tree phenology and architecture – species, age, leaf area and texture, crown structure, leaf emergence - and abiotic factors such as climate (Basset, 2001; Simon & Linsenmair, 2001). Trees, being structurally and ecologically complex, vary substantially in their phenology and architecture between different species and within individuals from the same species. For example, Doherty and Leather (1997) determined that tree architecture was one of the most crucial factors in influencing the distribution of spider communities and diversity within Scots pine stands in Scotland. Variation in tree substrate (e.g. bark, foliage etc.) can provide a range of habitats for invertebrates to colonise. Moreover, the microclimates, affected by biotic and abiotic drivers such as solar radiation can further influence the distribution of species and communities found there (Docherty & Leather, 1997; Jukes et al. 2002; Simon & Linsenmair, 2001). Light regimes are particularly important in influencing the distribution of herbivores, which aggregate in relation to foliage abundance (Poulson & Platt, 1989). Moreover, in temperate regions temporal climatic change is of particular significance, where high fluctuations associated with seasonal change influence the temporal and spatial distribution of resources and the fauna found there (Docherty & Leather, 1997; Moir et al. 2011; Rinker et al. 2001). As a result, this heterogeneity created in resources and abiotic factors within the trees has shown to shape a vertical and horizontal stratification of arboreal communities (Nadkarni et al. 2004).

Old-growth forests, such as the Caledonians, have been found to be highly important to some invertebrate communities, in particular rare and specialised. Saproxylic insects, such as fungus gnats (*Bradysia spp.*) and a diverse range of beetles (Coleoptera) are characteristic of mature and old-growth forests, with rich communities being found within mature European oak stands (Martikainen et al. 2000; Vodka et al. 2009). Much research has been carried out on invertebrate assemblages in the boreal forests of Nordic countries, which have experienced similar declines and fragmentations to Caledonian forests (Sippola et al. 2002). The studies mostly found that different forest attributes such as tree stands of mixed age and species, dead and decaying wood (standing or fallen) and lichen communities create many different microhabitats and niches for invertebrates to specialise in (Arnan et al. 2011; Esseen et al. 1996; Martikainen et al. 2000). Therefore a more 'specious and functionally diverse insect fauna is better supported in a complex habitat' (Arnan et al. 2011). Lichens for example, are a characteristic trait of old-growth temperate woodlands (Fig. 1) and are a valuable habitat to invertebrates, offering feeding, resting and breeding grounds in addition to providing a larger area of substrate for species to colonise (Esseen et al. 1996; Humphreys et al. 2002). Dead wood also provides as an important source to species. It can serve as a feeding ground for xylophagous and wood-boring beetles, among other insects, contributing towards the decaying process in trees and creating cavities for nesters such as the Apoidea *spp.* (Arnan et al. 2011; Sippola et al. 2002).



Figure 1. Lichen communities are commonly found on mature oaks (Dundreggan estate, Scotland: September 2011)

Entomological sampling can be difficult, due to the highly diverse habitat exploitation of invertebrates, making a complete census of a forest or even an individual tree immensely challenging (Humphrey et al. 1999). The collection of invertebrates, i.e. the trapping method and location of the trap largely depends on species behaviour within the tree canopy (Samways, 1995). For example, Bar-Ness et al. (2011) assessed novel and low-cost trapping methods. They clearly demonstrated the importance to tailoring to the specific classes of species under investigation (see also Proctor et al. (2002)). Therefore, it is crucial to use to ensure an adequate and representative sample of invertebrates within the forest stand (Odegaard, 2000; Samways, 1995).

Invertebrates, especially old-growth specialists, are highly susceptible to forest fragmentation and changes in abiotic and biotic conditions. This makes them ideal as potential tools in conservation, known as bio-indicators or surrogate measures (Christie et al. 2009; Didham et al. 1996; Humphrey et al. 1999). One of the reasons as to why they respond rapidly to disturbance is thought to be the result of a strong link between invertebrates and their host tree. These relationships leave the organism with little flexibility to recover in the face of disturbance (Didham et al. 1996). Sampling tree invertebrates as habitat indicators has been carried out before in the past (see Humphrey et al. (1999) for an example); however the application of these methods still needs further investigation.

The aims of this study were to investigate the invertebrate family diversity on selected Caledonian tree species using four different trapping methods – 1) to test their effectiveness and 2) to examine whether certain trap types are more taxa selective.

Methods

Study site

The study was carried out in the Dundreggan Estate of the Scottish Highlands, UK, situated North of Glen Morriston, West of Loch Ness (Fig. 2 & 3). The estate is approximately 4,000 hectares of upland habitat, with fragmented areas of native woodland and regeneration sites (Fig. 4). The majority of the woodland is open and overgrazed by red deer (*Cervus elaphus* L.) and sheep (*Ovis aries* L.). The estate has continuously been managed during the past years as a sporting estate and the westerly areas contain plantations of non-native conifers for commercial forestry practices. The estate has been designated as a Special Area of Conservation (SAC) and many species fall under the Biodiversity Action Plan (BAP). 'Trees for Life' is an established organisation partnered with the FC, RSPB and land owners. They carry out current management within the Caledonians with the long term aim to restore and reforest the uplands with native tree species (Trees for Life, 2011).



Figure 2. Location of Dundreggan Estate within Scotland (Google Maps, 2012).

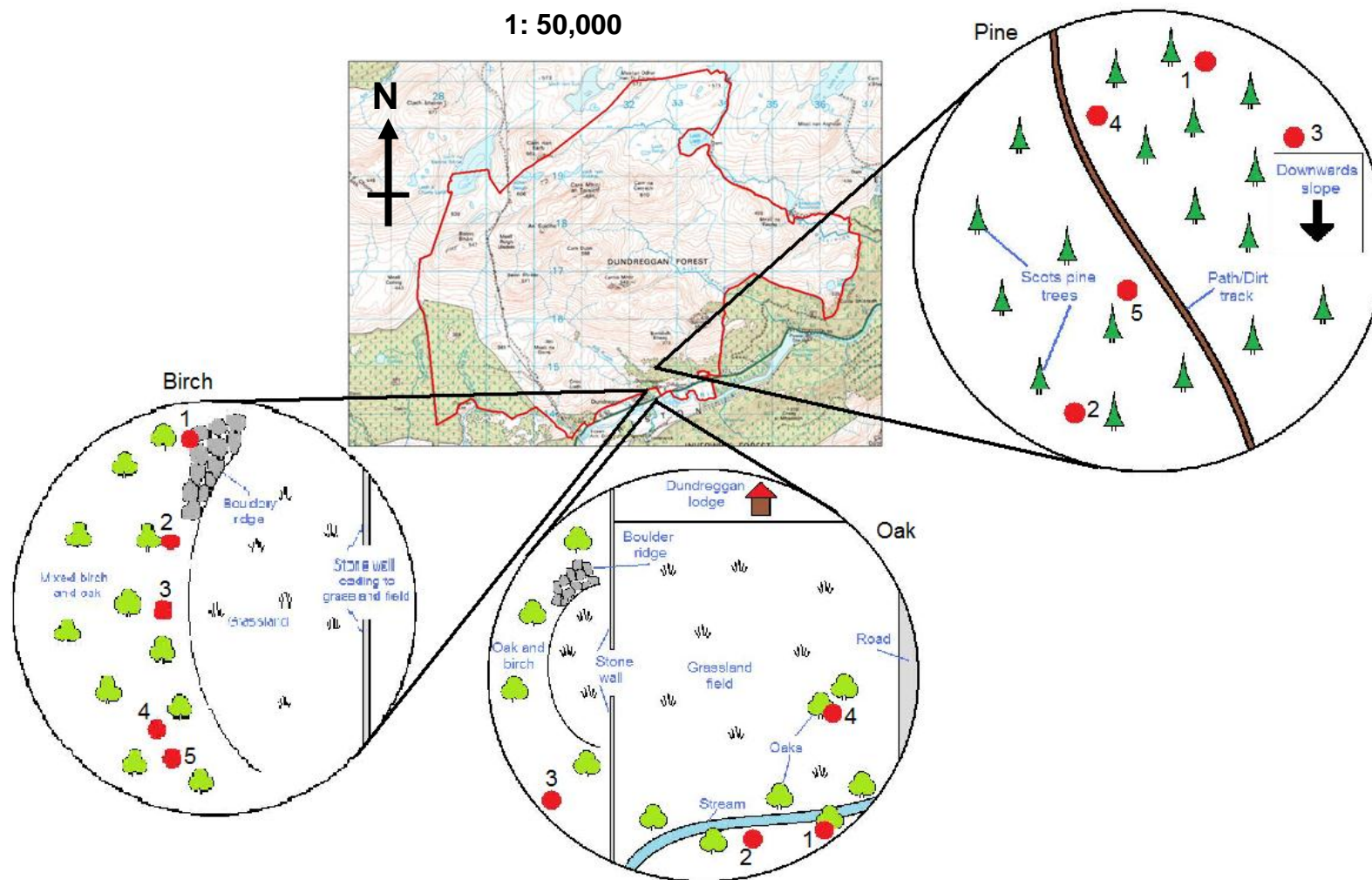


Figure 3. Dundreggan Estate boundaries (red line) and the characteristics of the study sites for birch, oak and pine tree locations. Trees indicated by red dots and numbers (Map supplied by Trees for Life).

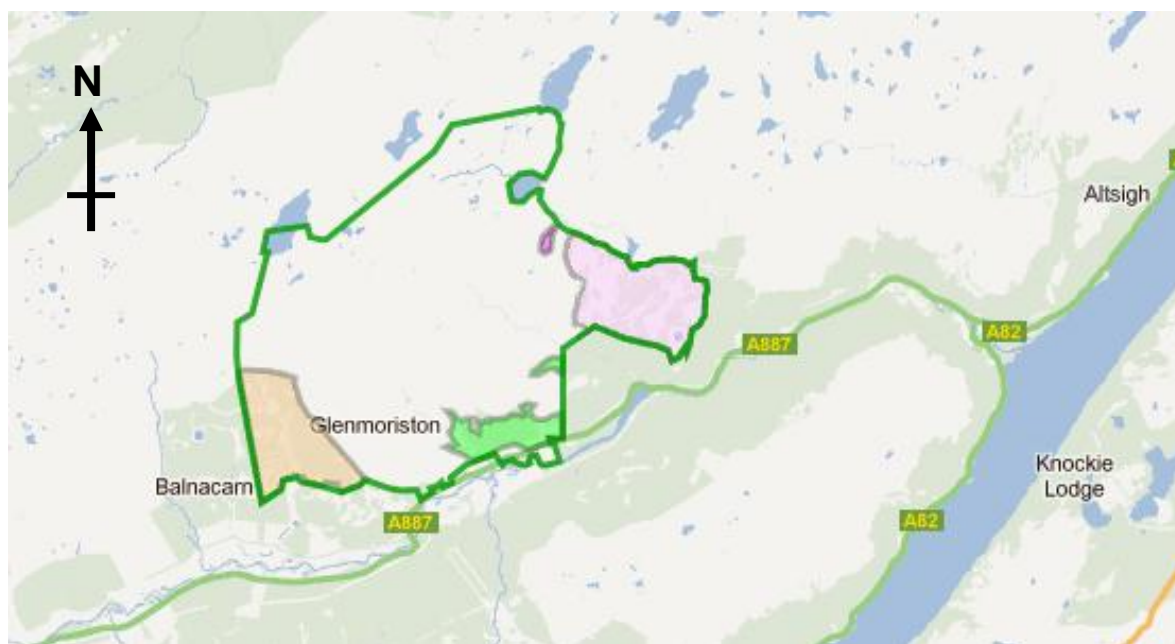


Figure 4. Habitat sector within Dundreggan Estate (orange – commercial plantation (mixed and native trees); green – ancient woodland; light pink – new native woodland planted in 2002; dark pink – dwarf birch enclosure) (TFL Volunteer, 2012)

Climatic observations during the period when data was collected showed a wetter and colder summer than in previous years. The late summer period (late August/early September) had frequent light showers throughout most days, with a few sunny intervals. The highlands experience a slightly cooler overall temperature than elsewhere in the UK with a mean annual temperature of 8.5°C and a mean annual summer temperature of 12.51°C (2002-2011). However, during the time of this study in the late summer period of 2011, the temperature was slightly cooler (11.40°C) and rainfall in the area was particularly high in 2011 for both the annual mean and the summer mean at 2005.1mm and 348.3mm respectively (Table 1).

Table 1. Mean annual and summer temperatures (°C) and rainfall (mm) for the last ten years (2002-2011) and the year 2011 only (Met Office, 2012).

Temperature	°C
Mean annual 2002-2011	7.6
Mean annual 2011	7.76
Mean summer 2002-2011	12.51
Mean summer 2011	11.4
Rainfall	mm
Mean annual 2002-2011	1723.51
Mean annual 2011	2005.1
Mean summer 2002-2011	329.22
Mean summer 2011	348.3

Study Trees

Three genera of tree were chosen to study, Scots pine (*Pinus sylvestris* L.), oak (*Quercus* spp. L.) and birch (*Betula* spp. L.). Oak in the area was predominately sessile (*Q. petraea*), but pedunculate oak may have also been present (*Q. robur*) and birch stands were a mixture of two closely related species, silver birch (*B. pendula*) and downy birch (*B. pubescens*). The 14 study trees (five birch, four oak and 5 pine) were chosen according to their location in either the forest or the adjacent grassland field on the Dundreggan Estate. Figure 3 demonstrates the locations of the study trees and the habitat characteristics of the area they were found in. Only mature trees were picked to keep age as constant as possible to allow for later comparisons. Trees were therefore selected based on their maturation status, canopy fullness and spread. Age was estimated using diameter at breast height (d.b.h.) and tree height as a surrogate. Differences in mean heights and d.b.h at a certain age between the different tree species were taken into account during the tree selection process. Table 2 evaluates which trapping methods were distributed within the different trees.

Table 2. The trapping methods used within the different study trees (F = fan trap, P = platform-pitfall-trap, T = thrashing, W = bubble-wrap-bark-trap).

Tree Code	Trapping methods		
	Birch	Oak	Scots Pine
1	F, P, T, W	F, P, T, W	F, P, T, W
2	F, P, T, W	F, P, T, W	F, T
3	F, T, W	F	F, T
4	F, T	F, P, T, W	F, P, T
5	F, P, T	N/A	F, P, T, W

Scots pines were all located within the forest on a slightly sloping terrain. This area was predominately pine with the occasional birch and an understory of bracken (*Pteridium* spp.), heather (*Ericaceae*) and bilberry (*Vaccinium myrtillus* L.). The d.b.h of the pines ranged from 260 to 347 cm (Fig. 5).

The birches were all situated along a boulder ridge adjacent to a grassland field at the base of the forest slope. These trees were in a more exposed and open environment, with an understory of bracken. The d.b.h of the birches ranged from 124 to 232 cm. The bark of the birch trees also often appeared to be very rough with large fissures to the texture (Fig. 6). Tree three of the oaks was also located along with these birch trees.



Figure 5. Pine tree five located within the forest



Figure 6. Location of birch tree three (left arrow) and two (right arrow)

Oaks one, two and four were located within the grassland field adjacent to the birch trees. These oaks were slightly more isolated from each other and the other sample trees. Oaks one and two were situated at the edge of the field alongside a small stream on a sloping embankment (Fig. 7), whilst oak four was located further from the stream and more central within the field. D.b.h for oaks ranged from 124 (being a slightly younger tree - juvenile to mature) to 348cm.

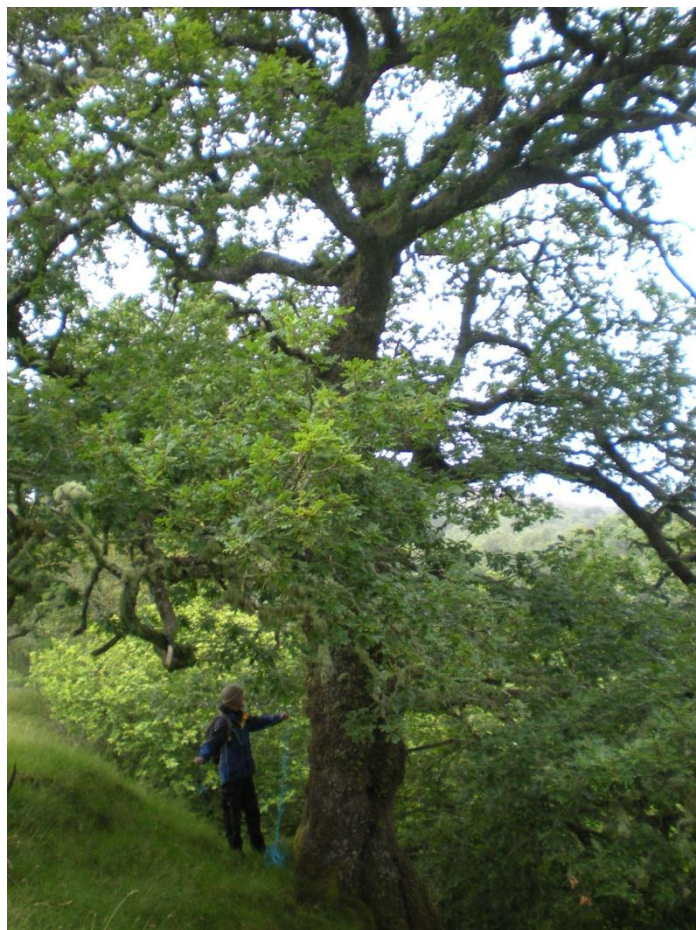


Figure 7. Oak tree two located on a small embankment at the field edge alongside a stream

Traps – distribution and location within the tree canopies

Fan-traps: Fan-traps consisted of a plastic cylinder with a fan inside and a screw top pot secured to the bottom. They were powered using a car battery placed at the bottom of the tree and attached via cord and crocodile clips (Fig. 8). The pot was filled to approximately a quarter with alcohol solution (70% ethanol) and was screwed to the attached lid. Fan-traps, also known as vortex traps, are thought to intercept flying insects making them potentially species specific. For this reason they were located high up in the canopy and close to the centre of the tree as recommended by Bar-Ness et al. (2011). They were raised into the canopy using string and subsequently secured in position. There were three fan-traps each placed during the early afternoon, one in each tree type, i.e. oak, pine and birch. The traps

were left for approximately 24 hours before being taken down. The collected sample was extracted and the trap reset for translocation to the next study tree.

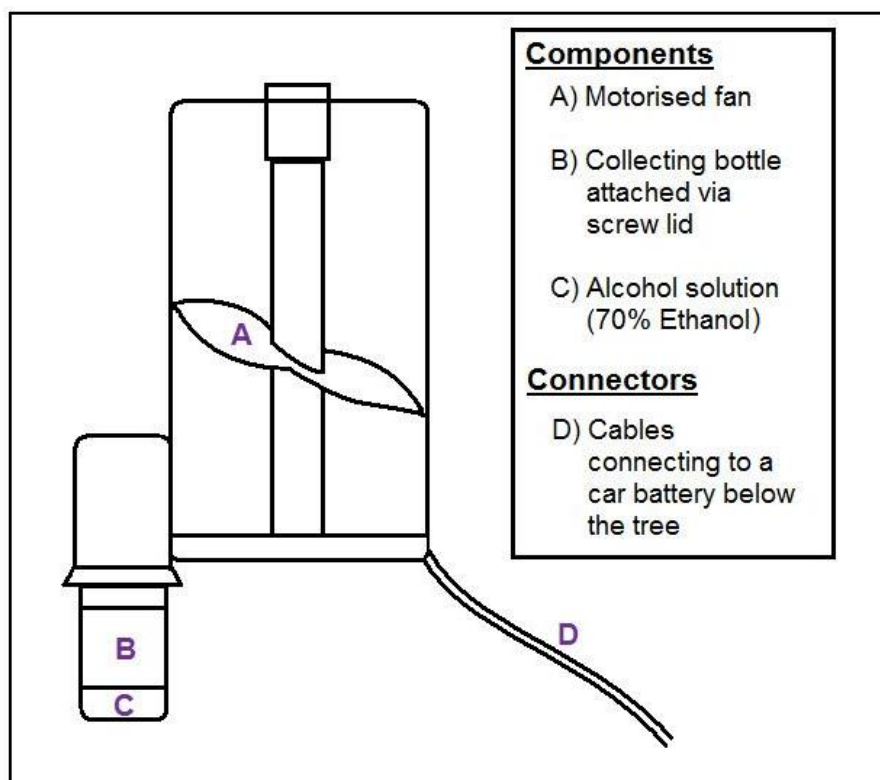


Figure 8. Fan-trap and its components

Platform-pitfall-traps: Platform-pitfalls consisted of a wooden platform with a hole in the middle (approximately 10cm across) and the rim of a screw top lid attached underneath (i.e. a hollowed out lid). A sampling pot, similar to the one described above, was filled with approximately 3cm² of antifreeze (Fig. 9). The antifreeze solution used in the traps contained ethylene glycol and was coloured with a blue dye. This was unintentional but did make the traps more visible during collection. Ethylene glycol was used in the pitfall traps as a killing agent as it contains cell toxins that poison the central nervous system of organisms (Braun et al. 2009; Leth & Gregersen, 2005). A string was attached to the four corners of the platform and tied at the top together to keep the platform level when hoisted into position. A total of 18 pitfalls was used, two placed in three of the subject trees for each species. In each tree the traps were set at different heights, one was within the lower branches of the tree, the other in the outer crown. Two heights were chosen because invertebrates are not uniformly distributed within the tree and so different assemblages are likely to occur at different heights (Samways, 1995). Additionally, pitfalls were positioned under dense foliage, in contact with the branches, to capture crawling insects using these habitats (i.e. branches and leaves). Pitfalls were checked each day to ensure they had maintained their position and were left in the trees for six days before being taken down. The collected contents was sieved and transferred into an alcohol solution.



Figure 9. (a) A platform-pitfall-trap set within the dense foliage of the canopy (b) Setting up a platform-pitfall-trap to pull into a birch tree using string.

Bubble-wrap-bark-trap: Bubble-wrap-bark-traps were used for three of the oak and birch and two pines of the selected trees. Pieces of bubble wrap, approximately 0.7 X 0.5 m, were laid against the tree trunk, roughly 0.5cm to a meter from the ground with the bubble side facing against the bark. A black bin bag was placed over the bubble wrap and attached securely to the trunk with string (Fig. 10). The bin bag was used to create a dark environment. Bark-traps were left for four days before the samples were collected using pooters (Fig. 11). Invertebrates collected were put into tubes filled with alcohol solution. Bark-traps enable sampling of the trunk fauna, identifying invertebrates that may be using the trunk as a 'highway' for accessing the canopy or ground, these are most likely to be poor dispersing and non-flying species (Proctor et al. 2002).



Figure 10. A bubble-wrap-bark-trap attached to oak tree

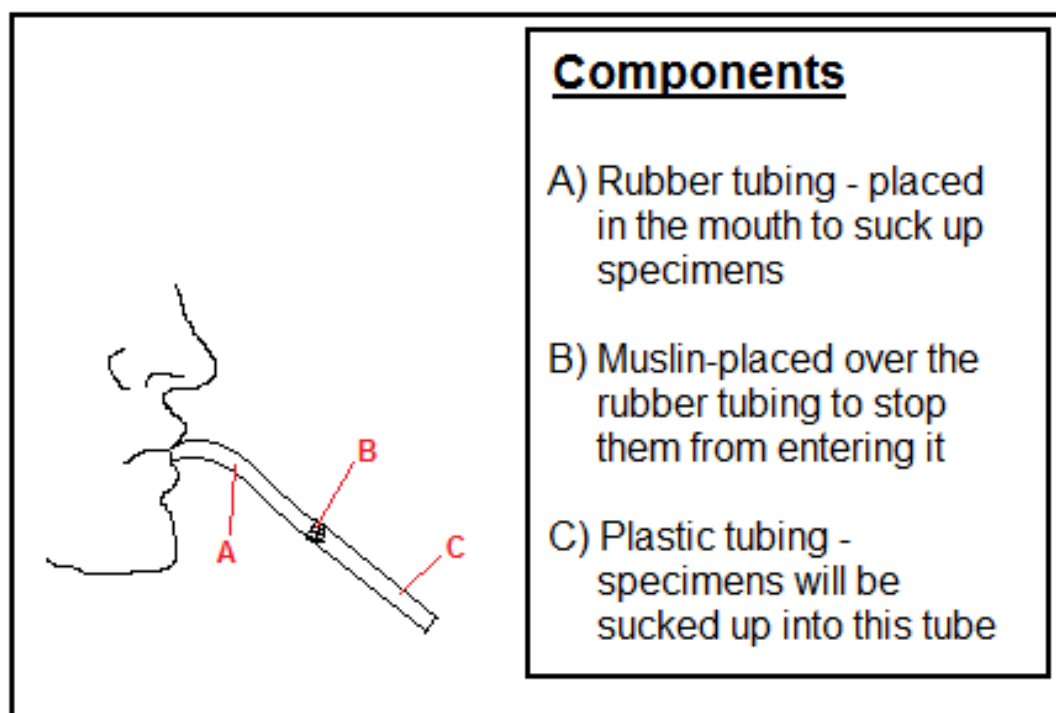


Figure 11. A pooter and its components

Thrashing: Thrashing was carried out on all five of the birch and pine trees and three of the oaks. Three of the lower primary branches of each tree were selected to carry out thrashing on. This was done using a large stick to hit the branches whilst an open umbrella was held underneath to catch the falling material and invertebrates. After thrashing the branch for a sufficient amount of time (approximately one to two minutes), the invertebrates caught in the umbrella were collected using a pooter (Fig. 11) and placed into a sample pot with alcohol. This method was used as an additive method to the pitfalls but was treated separately in the analysis.

Identification of samples

Identification of samples took place in a laboratory at Plymouth University. The invertebrates were identified to family level with the exception of Acari and *Cylisticus convexus*. Acari are extremely small and difficult to identify and were therefore lumped.

Data analysis

The program PC-ORD 6 was used to examine the differences in species diversity between tree and trap types using species evenness, richness, Shannon-Wiener and Simpson's diversity indexes. Moreover, a one-way and two-way cluster analysis was carried out to assess how invertebrate compositions between different tree and trap types grouped. The number of clusters was decided on following visual assessment of the cluster-diagrams. In addition, a NMS (Non-metric Multidimensional Scaling) ordination was used to further assess the data. A GLM (Generalised Linear Model) followed by Multiple Stepwise Regression was used to test whether any families had a significant association with a particular tree or trap type or both using the program R version 2.14.0. Environmental parameters were also tested using Spearman's

rank test. A Monte Carlo test was performed on the data to see which axis of the NMS ordination was statistically significant. Spearman's rank test then used the scores derived from the NMS to assess whether environmental variables measured influenced the species composition between individual treatments.

Two birch bubble-wrap-bark-trap samples were excluded from the NMS ordination as they were unsuccessful in catching specimens. In addition, the two sets of pitfall data for each individual tree were collaborated together for analysis to get results that tested the overall efficiency of this trapping method.

Results

A total of 71 families from 17 orders were encountered (See Appendix 1 for a full list of families). Table 3 shows the occurrence of the 20 most abundant families between different tree and trap types. The most abundant families were of Psychodidae and Cecidomyiidae (Diptera). These families were found at all three tree types and present in three of the four trap types (i.e. fan-traps, platform-pitfalls and thrashing). Psychodidae and Cecidomyiidae had the highest abundance off all 20 families and represented together with the other Diptera families c.40% of the total invertebrate abundance. The majority of these 20 families were found in all three tree types, with the exception of the family Cixiidae, which was exclusively found on birch trees. The most successful trapping methods, in terms of total families present, was thrashing and fan trapping (95% and 70% respectively), whereas, platform-pitfalls only collected 45% of the families and bubble-wrap-bark-traps only 20%.

Table 3. The 20 most abundant taxa found in samples, demonstrating presence or absence within tree type and trap type. Presence of taxa is represented by a cross

	Abundance	Tree Type			BWBT	Trap Type		
		Birch	Oak	Pine		FT	PP	T
Psychodidae	324	X	X	X		X	X	X
Cecidomyiidae	261	X	X	X		X	X	X
Linyphiidae	90	X	X	X	X	X		X
Phoridae	82	X	X	X		X	X	X
Chironomidae	62	X	X	X		X	X	X
Mycetophilidae	53	X	X	X		X	X	X
Phalangidae	48	X	X	X	X		X	X
Ichneumonidae	46	X	X	X	X	X		X
Ceratopogonidae	36	X	X	X		X	X	X
Sciaridae	36	X	X	X		X	X	X
Tetragnathidae	35	X	X	X	X	X		X
Cicadellidae	31	X	X	X			X	X
Mymaridae	18	X		X		X		
Lachesillidae	16	X	X	X		X		X
Geometridae	13	X	X	X				X
Tipulidae	13	X	X	X		X		X
Cixiidae	12	X						X
Acari	11	X	X	X		X		X
Thomisidae	11	X	X	X				X
Caeciliidae	10	X		X				X
Total	1208	20	17	19	4	14	9	19

A GLM was applied on the composition of families in relation to trap and tree types to assess if there were any significant associations between them. Only families with high abundances appeared to have a strong effect on the model and showed significance with treatments. Table 4 shows the combined effect of tree type and trap type on families. Associations that were positively significant with tree and trap types were predominantly Psychodidae and Cecidomyiidae (order: Diptera), also found as the most abundant families within this study (Table 3). They showed strong relations with oak and pine trees and with all trapping methods, with the exception of fan traps.

Table 4. Mixed-effect on family composition between the tree and trap treatments. Significant levels are as follows: P = 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05

Family	Tree type	Trap	Significant levels	Association – Positive/Negative
Psychodidae	Oak	Pitfall	***	Positive
Psychodidae	Pine	Pitfall	***	Positive
Psychodidae	Oak	Thrashing	***	Positive
Psychodidae	Pine	Thrashing	***	Positive
Psychodidae	Oak	Bubble Wrap	***	Positive
Psychodidae	Pine	Bubble Wrap	***	Positive
Phalangiidae	Oak	Thrashing	*	Positive
Cecidomyiidae	Oak	Pitfall	*	Positive
Cecidomyiidae	Pine	Pitfall	***	Positive
Cecidomyiidae	Oak	Thrashing	*	Positive
Cecidomyiidae	Pine	Thrashing	***	Positive
Cecidomyiidae	Oak	Bubble Wrap	*	Positive
Cecidomyiidae	Pine	Bubble Wrap	***	Positive

Invertebrate diversity and composition between tree species

Diversity indices for the three different tree types were generated using family richness and family evenness data (Table 5). Family diversity was highest in birch trees followed by oak and pine. However, family richness was highest in birch and evenness was found to be slightly greater in oak. Pine had the least invertebrate diversity, but had a greater mean number of families than oak. Overall, the difference in invertebrate diversity, richness and evenness between these three trees is fairly minimal.

Table 5. Diversity indices (D' = Simpson's diversity index; H = Shannon-Wiener diversity index), family richness (S) and evenness (E) for tree species and trapping methods. The highest scores from the Simpson's diversity index are highlighted in red.

	Mean	StD.	Sum	Min.	Max.	S	E	H	D'
Tree									
Birch	0.5956	2.487	42.29	0	16.43	8.4	0.77	1.622	0.716
Oak	0.4258	1.712	30.23	0	10.85	7	0.796	1.416	0.672
Pine	0.3427	1.334	24.33	0	9.333	7.5	0.67	1.369	0.586
Trap									
Fan	0.8471	3.891	60.14	0	26.64	7.6	0.718	1.388	0.666
Pitfall	5.63E-02	0.2898	4	0	2	2.7	0.53	0.721	0.389
Thrashing	0.4724	1.367	33.54	0	8.231	12.9	0.894	2.239	0.861
Wrap	8.45E-02	0.3701	6	0	2.167	3.7	0.791	1.106	0.589

The two-way cluster analysis of the different tree types, with regards to the family composition revealed a division into three main clusters (Fig. 12). Cluster one consisted of a mix of birch (55.56%) and oak (33.33%) with one single pine (11.11%). Clusters two and three were predominantly composed of pine stands (80%), with the exception of one oak (20%). Family composition showed no clear grouping between tree types, with most taxa being found in all tree types. Invertebrate families show correspondence more to taxa similarity (vertical alignment) rather than to tree clusters (horizontal alignment). The NMS ordination plot in Fig. 13 also showed that there was no distinct similarity in the community composition between tree stands of the same species. In addition, invertebrate orders did not greatly differ between different tree types (Fig. 14). Of each tree sampled, the community is composed mainly of Diptera (c.50%) and a smaller percentage of Aranea families (c.8-19%). However, noticeable differences between tree types are found in birch stands, where the community is composed of a large proportion of Hymenoptera (c.9.64%) and in oak stands where c.8% of the community composition is made up of Opiliones (harvestmen).

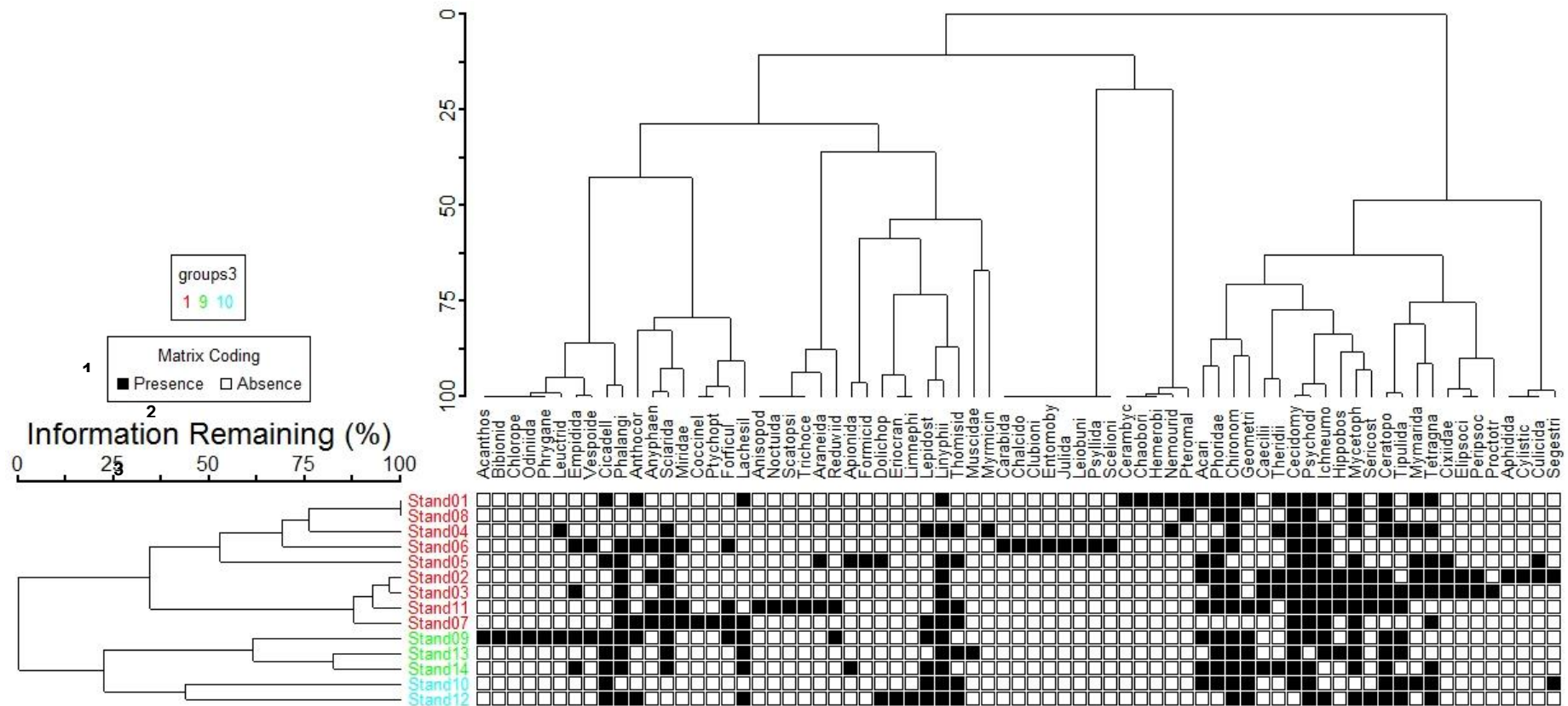


Figure 12. The two-way cluster analysis is based upon a) the species composition between different trees (left) and b) how they correspond to the individual families (top). The black squares highlight presence and absence of families (top) in correspondence to the tree clusters (left.). The tree clusters are coloured as follows; red = cluster 1 (1), green = cluster 2 (9) and blue = cluster 3 (10). The tree 'Stands 01-05' related to birch, 'Stands 06-09' to oak and 'Stands 10-14' to pine.

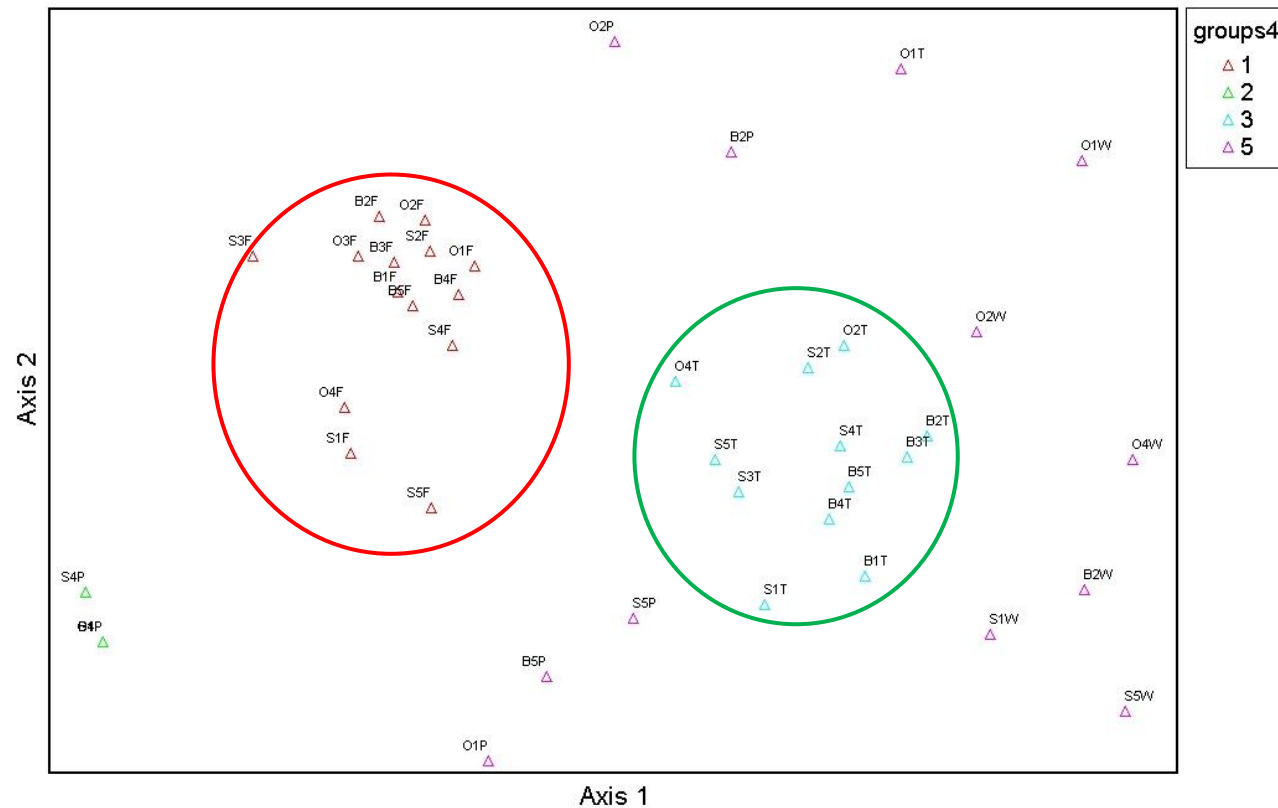


Figure 13. The NMS (Non-metric multidimensional scaling) ordinated the samples with the different treatments (i.e. trap type and tree type) into a two-dimensional plot based upon the variance in family composition. Samples most similar to each other are grouped closer together, whereas, samples most dissimilar are grouped further apart. Fan traps (red circle) and thrashing (green circle) showed distinctive groupings, indicating that the family composition of different trapping methods is more similar to each other than their response to tree type. Labels are as follows; B = birch, O = oak, S = pine, F = fan trap, P = platform-pitfall, T = thrashing, W = bubble-wrap-bark-trap.

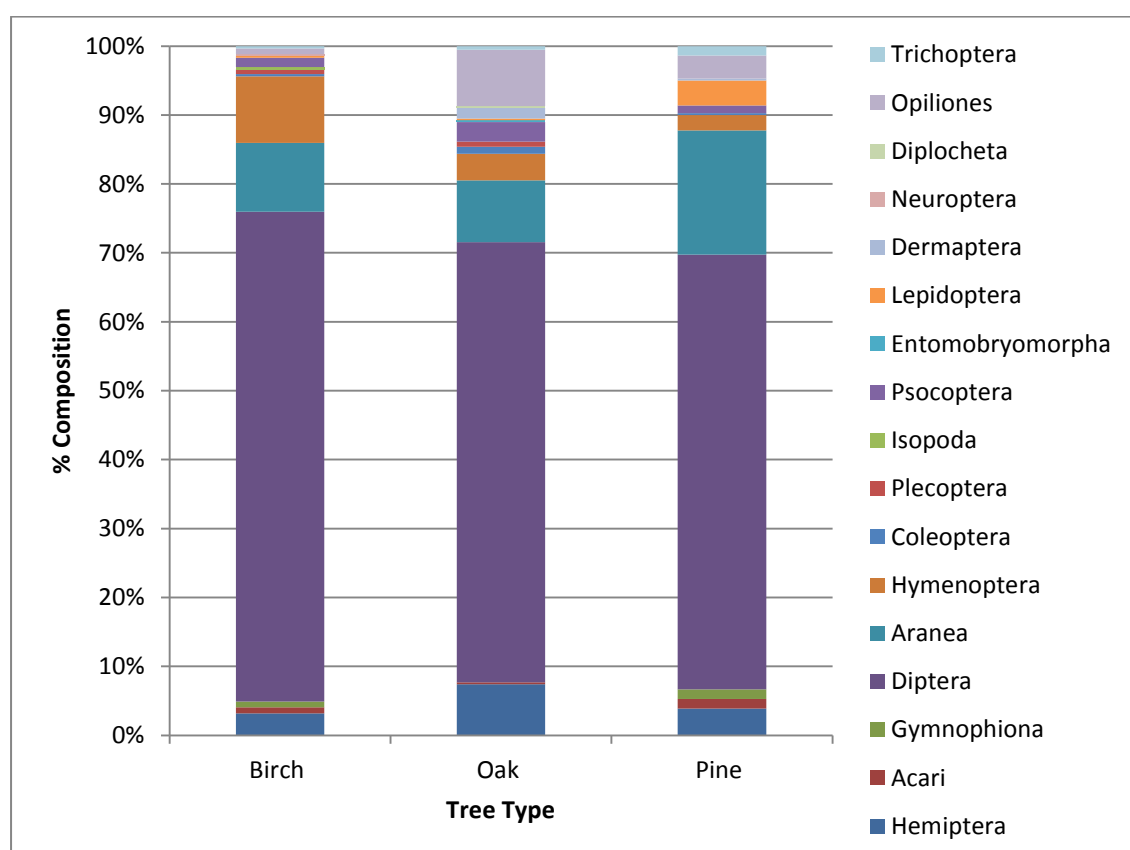


Figure 14. The composition of invertebrate orders found in different tree types: birch, oak and pine.

Table 6 shows the GLM results of the single effect of tree type on families. Only two Diptera families showed any significant associations with tree types, oak and pine. These associations were negatively significant, therefore as the number of pines and oaks sampled increased, the number of individuals from these families decreased. All results in Table 6 are shown to be highly negatively significant with a 95% confidence interval ($P = >0.001$).

Table 6. Mixed-effect on family composition between the different tree types only. Significant levels are as follows: $P = 0$ '***' 0.001 '**' 0.01 '*' 0.05

Family	Tree Type	Significant levels	Association - Positive/Negative
Psychodidae	Oak	***	Negative
Psychodidae	Pine	***	Negative
Cecidomyiidae	Oak	***	Negative
Cecidomyiidae	Pine	***	Negative

Catch efficiency between trapping methods

Diversity indices for the four different treatments showed that diversity in the thrashing treatment was much higher than for the other three methods (Table 5). Thrashing not only had a greater number of families then other treatments, but the

individuals within the community were also more evenly distributed among families. The pitfall treatment showed the lowest diversity of all trapping methods, where family richness was approximately 75% less than in the thrashing treatment.

A division into two groups between trapping methods was detected from the cluster analysis. Cluster one consisted entirely of fan-traps, the other contained a mixture of the three remaining trapping methods. Within the second cluster there were separate groupings of thrashing and bubble-wrap-bark-traps, showing greater similarity within these trapping methods than with others. From the two-way cluster analysis (Fig. 15), cluster one pointed towards a great similarity in family composition between all fan-traps. Family composition for fan-traps was dominated by flying invertebrates; in particular Diptera families such as Chironomidae and Phoridae (see also Table 3). Cluster two had little distinct patterns with regards to family composition. All trapping methods showed preference of catching non-flying invertebrates and only a few traps caught Diptera families only. However, the grouping of thrashing does show that a great number of specimens caught were Aranea (spiders) such as Linyphiidae, Tetragnathidae and Thomisidae. Invertebrate order composition between trap types is displayed in Fig. 16. Diptera composition was highly affected by trap type, specifically fan-traps (>95% Diptera), whereas other trapping methods predominantly caught non-flying invertebrates. Thrashing and bubble-wrap-bark-traps had communities of a more diverse order range and had high abundances of Aranea and Opiliones.

The NMS results presented in Fig. 13 indicated a similarity between individual samples and trap type. The treatments thrashing and fan-trapping grouped in the ordination plot distinctively. Both treatments are dissimilar from each other in terms of their position within the ordination space but show strong groupings of sample replicates within. Other treatments showed more spread across the matrix, indicating very low similarity between these samples. This NMS ordination supports the two-way cluster analysis and signifies that fan-trapping and thrashing may show higher family composition similarity than other methods.

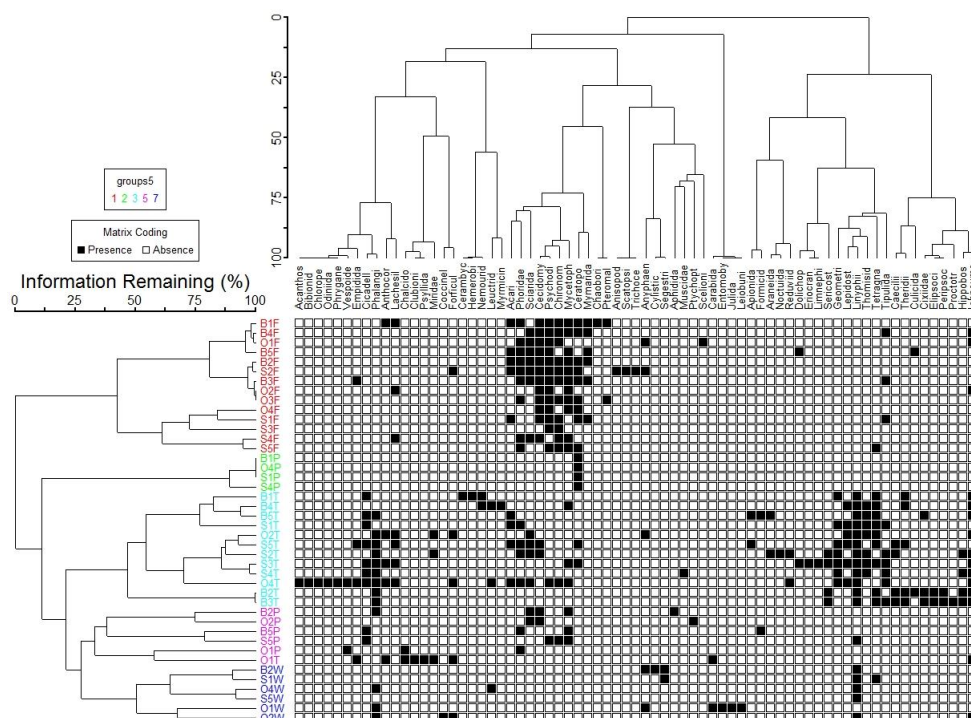


Figure 15. The two-way cluster analysis is based upon a) the species composition between different trapping methods (left) and b) how they correspond to the individual families (top). The black squares highlight presence and absence of families (top) in correspondence to the trap types (left). The trap clusters are coloured as follows; red = cluster 1 (1); green/blue/pink/purple = cluster 2 (2,3,5,7). Labels are as follows; F = fan-trap, P = platform-pitfall, T = thrashing, W = bubble-wrap-bark-trap.

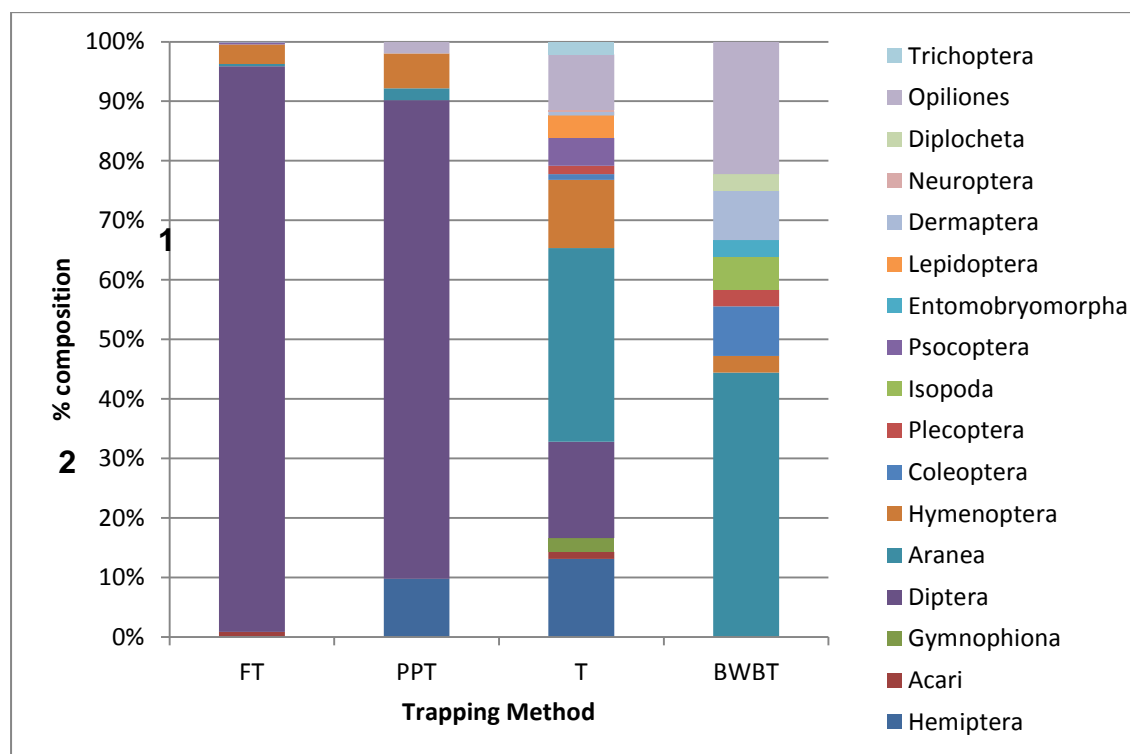


Figure 16. The Composition of invertebrate orders found in four different trap types (FT = fan-trap; PPT = platform-pitfall-trap; T = thrashing; BWBT = bubble-wrap-bark-trap).

Table 7 shows the single effect of trap type on families from the GLM analysis. Families showing significant associations with trapping methods were predominately from the order of Diptera to thrashing, bubble-wrap-bark-traps and pitfall trapping methods. However, these were negatively significant, whereas thrashing was found to have a positively significant effect on Linyphiidae, Tetragnathidae (Araena) and Ichneumonidae.

Table 7. Mixed-effect on family composition between the different trap types only. Significant levels are as follows: P = 0 '***' 0.001 '**' 0.01 '*' 0.05

Family	Trap	Significant levels	Association - Positive/Negative
Tetragnathidae	Thrashing	*	Positive
Psychodidae	Pitfall	***	Negative
Psychodidae	Thrashing	***	Negative
Psychodidae	Bubble wrap	***	Negative
Phoridae	Pitfall	*	Negative
Phoridae	Thrashing	**	Negative
Phoridae	Bubble wrap	**	Negative
Linyphiidae	Thrashing	*	Positive
Ichneumonidae	Thrashing	**	Positive
Chironomidae	Pitfall	*	Negative
Chironomidae	Thrashing	*	Negative
Chironomidae	Bubble wrap	*	Negative
Cecidomyiidae	Pitfall	***	Negative
Cecidomyiidae	Thrashing	***	Negative
Cecidomyiidae	Bubble wrap	***	Negative

Environmental parameters

Spearman's rank correlation coefficient was used to test environmental data collected for individual trees (Table 8). This showed whether family composition in the trees was driven by environmental variables using scores derived from the NMS ordination (Fig. 13). The following environmental variables were tested; tree height, canopy spread and the d.b.h. Only axis 1 of the NMS ordination was included in the Spearman's rank test as axis 2 showed not to be statistically significant following Monte Carlo procedure and was therefore excluded. Table 7 showed that family composition for groups closer to axis 1 is mainly explained by canopy spread ($r_{40} = 0.313$, $p < 0.05$), this primarily includes thrashing and bubble-wrap-bark-traps as the NMS ordination showed grouping of trap types as opposed to tree type. The other trapping methods grouped closer to axis 2 cannot be explained by canopy spread and are therefore likely to be affected by other environmental parameters that were not measured (e.g. wind speed, temperature etc.). However, there are significant levels between other environmental parameters not in relation to the axis, all showing positive significant correlation: 1) as tree height increases, canopy spread and d.b.h increases and 2) as canopy spread increases, d.b.h. increases.

Table 8. A Spearman's rank correlation test was used to test if environmental parameters measured (tree height, canopy spread and d.b.h) explained the family composition in relation to axis one in the NMS ordination (Fig. 13). The critical value for two-tailed r_s (the correlation coefficient) at 0.05 was 0.313, values above this coefficient are significant (in bold).

	Axis 1	Height	Canopy spread	DBH
Axis 1	1			
Height	0.149	1		
Canopy spread	0.603	0.429	1	
DBH	0.247	0.617	0.691	1

Discussion

The data collected from this study show that there is little difference in invertebrate diversity and composition found between birch, oak and Scot's pine trees. However results do indicate that pine supports the least family diversity and their invertebrate community is less similar in composition compared to birch and oak stands. Consequently, this study was unable to provide strong evidence to determine whether invertebrate communities differ between tree species. However this study showed to be effective in demonstrating taxa relation to trapping methods. The four trapping methods used showed to be highly taxa specific, where flying insects were predominately caught by fan-traps and non-flying insects were caught by traps with direct contact to tree substrate. Canopy spread was unable to describe family composition found within all tree and trap types, showing most association with thrashing and bubble-wrap-bark-trap methods. Therefore, other environmental parameters are likely to have a much stronger influence on family composition found within tree and trap types, such as temperature and exposure levels.

Seasonality

Firstly, the results showed that little difference between family diversity was found between tree types. Climatic data for the area at the time of the study showed that the summer was colder and wetter than the average temperature and rainfall for the last ten years (Met Office, 2012), which may have had an effect during the sampling period. In addition, the sampling was carried out during late summer (late August/early September) and seasonality has been shown to have large effects on an invertebrate's temporal distribution. In regions where climate is fairly predictable and conditions remain considerable constant throughout the year (e.g. the tropics), invertebrate populations are expected to show low fluctuations in abundance and species richness. However, in temperate regions such as the highlands, where seasonality is present, climatic conditions are extremely important parameters in influencing invertebrate diversity (Pinheiro et al. 2002). Climate has a direct influence on food availability; in the case of herbivores this is the abundance and emergence of leaves, which in turn consequently influences predatory and parasitic invertebrates which often feed on or utilize these herbivores. Invertebrate abundance peaks soon after the emergence of foliage as most show high preference for younger leaves (Kai & Corlett, 2002; Leksono et al. 2005). These young leaves are highly nutritious and hydrating, opposed to older, mature leaves which develop toughness in lignin and fibre (Rinker et al. 2001). Much research of seasonality on species distribution has been carried out in Asia. In the temperate deciduous forests of Japan, abundances of herbivorous flying beetles peaked during early summer

(May/June) (Leksono et al. 2005) and declined in winter, similar results were seen in Hong Kong studies (Kai & Corlett, 2002). However predatory beetles and Diptera showed little seasonal change and maintained constant fluctuations throughout the year (Kai & Corlett, 2002; Leksono et al. 2005). In tropical savannahs, where seasonality is characterised by rainfall, invertebrate abundance is at its highest during the rainy season and low in the dry season. Leaves become limited by the availability of water vital to their growth and reproduction and decline in nutritional value (Braby, 1995). Within the UK, stands of commercially managed Scot's pine show seasonality in a range of taxa; Hymenoptera, Coleoptera, Lepidoptera and Homoptera. Spring provides an ideal climate for many of these invertebrates, in particular sawflies (Symphyta) (Simandl, 1993). Therefore, invertebrates occurring in these seasonally changing habitats are influenced by resource availability and during stressful times (e.g. cold conditions) are likely to show adaptive behavioural responses and strategies. These may include being inactive for a period of dormancy, demonstrate diapauses until favourable conditions appear or migration during adverse conditions (Pinheiro et al. 2002). Consequently, a turnover of species is expected of invertebrates as they depend upon when and where the resource they utilize is most abundant (Ober & Hayes, 2008; Pinheiro et al. 2002). In addition, resource availability can influence invertebrate breeding patterns as abundant resources for offspring strongly influence survival rates. For example, Coddington et al. (2009) found that many adult spiders are scarcely found outside their breeding periods, potentially using the tree as a seasonal migrant habitat (Colwell & Coddington, 2012). This may therefore additionally contribute to low differences in family diversity between tree types in this study as the majority of seasonal migrants will have most likely vacated the area during late summer due to limited resources and remaining populations likely to be permanent residents.

Habitat Heterogeneity

Species richness, abundance and distribution are highly influenced by the heterogeneity of the habitat. Once thought to be homogenous, tree canopies are now recognised as structures with high architectural complexity, containing a variety of microhabitats which enables the colonisation and specialisation of a range of niches (Lavandero et al. 2009; Lowman, 2001). Heterogeneity can occur through the spatial distribution of resources, differential substrates and from the influence of abiotic conditions. Consequently, niches become occupied by invertebrates differing in feeding guilds and resource utilisation, enabling the coexistence of species within a habitat (Lavandero et al. 2009; Powell et al. 2011). This study found that species diversity was highest in birch and oak trees (respectively) and lowest in Scot's pine. Scot's pines were originally considered to be one of the least structurally complex tree species within the coniferous community. They have thin, sparse canopies, reduced leaves in the form of needles and create relatively open stands (Ishii & McDowell, 2002), potentially reducing the capacity for habitat diversity (Kuuluvainen et al. 1998). Although, more recent studies emerging are suggesting that this may not be the case and Scot's pines are more heterogeneous than originally thought (Kuuluvainen et al. 1998). Therefore this low diversity, compared to birch and oak, may be more related to the palatability and phytochemical attributes of the tree types, which influence herbivore distribution and abundance in particular. Compared with coniferous species, deciduous trees are lower in lignin and resin contents, which are difficult for many invertebrates to consume (Carlisle & Brown, 1968; Ober & Hayes, 2008). Deciduous also contain a higher mineral content than conifers, rich in

nitrogen, which is often the limiting factor for many invertebrates as they use it for growth and ultimately important in overall survival (Ober & Hayes, 2008). Lavandero et al. (2009) studied the phytochemical make-up of different tree species from the genus *Nothofagus* and found that the species most chemically unique and high in volatile turpentine supported fewer invertebrate species, which were also more specialised. These differential properties between deciduous and coniferous trees may explain why the two-way cluster analysis showed one grouping of mixed birch and oak and another of predominately pine trees.

Birch trees were shown to be more diverse in invertebrate families than oak, however much literature recognises oak trees as being highly specious, particularly in mature and old aged trees. Oaks demonstrate a variety of traits that create high heterogeneity within the canopies, contributing towards supporting diverse communities by providing a range of various niches to be exploited (Ohsawa, 2007). One particularly important feature of oak trees is the epiphytic communities they support, providing feeding and breeding grounds and a resting habitat to fauna (Humphreys et al. 2002). Cruz-Angon et al. (2009) found that trees within a Mexican coffee plantation with epiphytic communities possessed more diverse invertebrate communities than without. Epiphytes, such as lichens and bryophytes, are often found inhabiting old trees and over time they can accumulate a biomass of up to 44 tonnes per hectare, as they can grow to form mats across the substrates they colonise, increasing surface area. They also form localised microhabitats where they accumulate soil in tree crevices, adding organic matter for detritivores to exploit, and store moisture, creating humid environments. Predatory invertebrates such as spiders (Aranae) and Centipedes (Chilopoda) have also been found to be commonly associated with tree epiphytes (Diaz et al. 2012). Pine trees however, have been found to have lower associations with lichens as they have a lower capacity to hold water, higher evaporation rates and have a lower pH than oaks. In addition their bark easily flakes making it an unstable habitat for epiphytes to colonise (Humphreys et al. 2002). Moreover, older oaks possess high quantities of dead wood and cavities within the trees which are important habitats for sustaining abundant communities of saproxylic insects and cavity nesting fauna (e.g. arboreal ants) (Powell et al. 2011). The GLM results found negative significant associations between the families Cecidomyiidae and Psychodidae (order: Diptera) with oak and pine trees, this suggests the oak and pine trees are unsuitable for these invertebrates. Although significance was not found with these families and birch, Cecidomyiidae have been found to be associated with denser canopy cover, which appeared to be highest in birch trees (Dodd et al. 2012).

Habitat heterogeneity has also been linked to MacArthur and Wilson's theory of Island Biogeography (IBT) which assumes that larger areas contain higher heterogeneity, able to support higher species richness, maintain larger populations and therefore support more specialists (MacArthur & Wilson, 1967; Ozanne et al. 2000). Stands of trees that are more taxonomically similar, such as in chemical attributes and properties are thought to be able to support large populations of species. They can create large areas of continuous habitat, which can be particularly beneficial to host-specific species, by allowing individuals to switch from one host tree to another with fewer dispersal difficulties (Lavandro et al. 2009). This may explain the higher diversity found in birch trees to oaks, as birch stands were distributed close together. Whereas oak trees were very spread out across the area

and more isolated from one another as well as other trees. However, this is contrary to research carried out by Kuuluvainen et al. (1998) in boreal forests that suggested stands of mixed tree species and age and a developed understory are likely to pose higher species richness. This therefore could explain lower family diversity in pine trees as they were situated in an area of the forest that was predominately Scot's pine stands and had a relatively sparse understory and ground-layer compared to that of the birch location.

Edge effects

The sampled birch trees were located along an exposed boulder ridge, bordering a grassland habitat. In much literature this exposure is important in influencing species composition and can often create adverse conditions for invertebrate colonisation. However, despite this, these birch trees were found to support the highest diversity. Alternatively, oak tree diversity may be explained by these exposure effects as these trees were more isolated from other stands. 'Edge effects' is often the term given to this natural process, where the boundaries between adjacent habitats are influenced by abiotic and biotic parameters, consequently creating differential conditions between the exterior and interior of the habitat (Foggo et al. 2001; Murcia, 1995; Ozanne et al. 2000). During recent years human land use change has exacerbated this process as the fragmentation and isolation of habitats is increasing and remains of natural habitats are adjacent to matrixes of a more simplified landscape (e.g. agricultural land) (Foggo et al. 2001; Ohsawa, 2007). This isolation of trees and habitats can expose canopy invertebrates to harsh environmental and climatic conditions (e.g. wind speed and insolation (solar radiation)) (Ozanne et al. 2000). The magnitude of these effects are often dependent upon the size of the fragment, degree of exposure and the environment of the adjacent habitat (Foggo et al. 2001), as edge effects have been seen to still have effect 50m within the fragment (Murcia, 1995). Faunal compositions within these edges can strongly reflect its interaction with the adjacent matrix (Ozanne et al. 2000). Ozanne et al. (2000) found that more isolated Scot's pine trees in a heathland matrix were containing individuals of the heathland spider, *Scotina gracilipes*. This may also be evident in this study as the sampled oaks, which were most isolated, were found to support the highest abundances of the harvestmen Phalangidae and Leiobunidae (Opiliones), which are known to be inhabitants of ground and field layers, which was characteristic of the surrounding matrix (Adams, 1984; Todd, 1949).

Invertebrates are highly susceptible to habitat change and there is evidence that low-tolerant species occur less in these edge habitats or if present possess high mortality rates (Didham et al. 1996). This therefore has led to assumptions being made that species occupying edge habitats are often specialists and have adapted to cope with the associated harsh conditions. Alternatively, these communities may be invertebrates with good dispersal abilities, enabling them fast escape when conditions change for the worst (Foggo et al. 2001). Ozanne et al. (2000) found that edge communities, in isolated British Scot's pine stands, supported a lack of juvenile spiders and those present of the family Theridiidae had mortality rates two and a half times higher in smaller pine stands. Juvenile invertebrates are highly susceptible to climatic and environmental change, lacking the large body adult's possess and use as a buffer to protect against conditions that may cause desiccation to the individual - i.e. hot, windy and low levels of humidity (Janzen & Schoener, 1968; Ozanne et al. 2000). This may additionally affect the distribution and abundance of predatory invertebrates along these habitats that often feed on younger prey, as their soft

bodies supply an easy resource supply of liquid (Janzen & Schoener, 1968). Therefore edge effects are likely to have affected the diversity of families found within oak trees.

Trap efficiency and specificity

All trapping methods were successful in catching invertebrates and a total of 1350 specimens were caught from 71 different families. The majority of specimens caught were from the order Diptera contributing to c.66% of the abundance. Diptera are an extremely diverse and mobile order and most species have large habitat ranges. This enables them to occupy a variety of niches and they often show localised aggregations of individuals within the same species (Levesque-Beaudin & Wheeler, 2011). This is concurrent with studies showing that although many herbivorous invertebrates show seasonal changes in abundance and distribution, Diptera are often fairly stable throughout the year (Kai & Corlett, 2002). However, Diptera distribution and composition, and the environmental parameters that influence it, are understudied and more research has yet to be done in this area (Levesque-Beaudin & Wheeler, 2011).

Trapping methods showed indications of being taxa specific in their collection of invertebrates. The two-way cluster analysis showed fan traps to be distinctly dissimilar in its community composition than the other three treatments (bubble-wrap-bark-trap, platform-pitfall and thrashing), primarily consisting of Diptera families (95% compositions). This was opposed to a diverse range of non-flying invertebrates found in thrashing and bubble-wrap-bark-traps. The probability of capture within a trap varies greatly between invertebrate species depending on factors such as their dispersal ability, habitat requirements and behaviour (Colwell & Coddington, 2012; Levesque-Beaudin & Wheeler, 2011), enabling trapping methods to be highly specialised in catching certain taxa. This can be via their design or position within the habitat (Pinheiro et al. 2002). In this study fan traps were placed around the mid-level to upper canopy, without contact to the tree itself, with the intention to 'suck' in invertebrates that passed over the trap. Other traps similar to this are specifically designed for the purposes of flight-interception and found that a very small number of orders accounted for most of the species composition (86.5%): Diptera, Hymenoptera, Coleoptera and Homoptera (Carrel, 2002). Most Diptera families have also been found to accumulate close to the tree and tend to concentrate at mid-level in the canopy; this may additionally explain the captured specimens within the fan-traps (Peng et al. 1992). However, GLM results showed no significant associations of families with fan traps despite there seeming to be an effect of fan-traps on these Diptera families (shown in Fig. 15). This is because the number of individual families associated with these traps was low, most likely due to a lack of sampling data via replicates.

Bubble-wrap-bark-traps also showed some degree of specificity to invertebrate taxa, capturing three orders, almost wholly exclusive to bubble-wrap-bark-traps, of earwigs (Dermaptera), springtails (Entomobryomorpha) and millipedes (Diplocheta). These orders comprise of mainly nocturnal invertebrates that require dark, moist and secluded habitats during daylight hours. The bark of trees ideally creates these properties for inhabitants and is additionally reflected under the bubble-wrap-bark-traps (Gordh & Headrick, 2001). Whereas thrashing samples, also consisting mostly of non-flying invertebrates, showed high proportions of spiders (Araneae), ants (Hymenoptera) and booklice (Psocoptera). This is concurrent with results from beating

methods carried out in the seasonal temperate forests of Hong Kong during August-October (Kai & Corlett, 2002).

Platform pitfall traps are commonly used traps in invertebrate sampling and often effective in catching large numbers of surface-active invertebrates from a range of taxa (Ward et al. 2001). However, the pitfalls used in this study showed lowest family diversity. Mommertz et al. (1996) suggested factors that may influence the effectiveness of pitfall traps, these included trap diameter, construction material and preservatives used, as well as species behaviour and environmental influences. Of particular importance, the pitfalls used in this study contained a solution of ethylene glycol which was blue in colour. Some research has found colours to be attractants to species, such as Miridae, found to be attracted to hues of green, blue, clear and translucent (Blackmer et al. 2008; Woodcock, 2005). However pitfall traps were not found to capture any Miridae and therefore the blue colouring may be acting as repellent to invertebrates instead.

Consequently these trapping methods are able to loosely distinguish the microhabitats certain taxa are occupying and give a minor indication to vertical stratification of invertebrates within the trees (Pinheiro et al. 2002; Sobek et al. 2009).

Environmental Parameters

Results from the Spearman's rank test showed that canopy spread explained some of the family composition found within the thrashing and bubble-wrap-bark-trap treatments. The spread of a canopy is important in creating connectivity between trees within a habitat, providing a continuous environment for the dispersal of invertebrates between trees (Lavandero et al. 2009). This connection is particularly important for invertebrates that lack the ability to fly, which may indicate as to why canopy spread was most influential in thrashing and bubble-wrap-bark-traps, opposed to fan-traps. Studies conducted on canopy connectivity, by Powell et al. (2011), found that fewer species of arboreal ants coexisted in individual trees when connectivity was low. In addition, it was recognised that there was strong correlation between canopy connectivity, tree size and species richness per tree (Powell et al. 2011). This may also be indicative in this study as there was positive correlation between canopy spread and tree size (measured as tree height and d.b.h.). Therefore canopy spread is highly dependent on tree growth; as tree height and d.b.h increases, canopy spread increase, which may consequently allow higher rates of habitat connectivity.

Other parameters that were not measured during this study are likely to account for the family composition and richness found within other trapping methods. This primarily includes the degree of exposure to vertical and horizontal environmental processes. In addition to the influence of edge effects, exposure is linked to light levels and solar radiation intensity, temperature, wind speed, canopy density and humidity levels. These parameters can become interlinked and influence each other, for example, high exposure levels to insolation in the upper crown can increase temperatures and evaporation rates, reducing the amount of trapped moisture (humidity) within the crown, consequently cause invertebrates to desiccate (Foggo et al. 2001). Alternatively, wind speed can have similar effects as it increases in velocity, reducing humidity levels. Humidity levels within the canopy have been shown to largely fluctuate throughout the day, sometimes showing a reduction of

70% at midday to night humidity and are of particular importance as they provide invertebrates with a source of hydration (Nadkarni, 1994). In addition, temperature has been shown to not only influence foraging behaviour but also ovipositing within insects (Rinker & Lowman, 2004). Consequently, communities often depend upon species tolerance levels to environmental factors and many insects in temperate regions have been found to avoid the canopy crown during periods of high temperatures (July/August) to avoid the risk of desiccation (Leksono et al. 2005). These parameters are likely to have a particularly strong influence on species composition in fan traps as they were placed near the crown of the canopy and were considerable more exposed to environmental parameters such as insolation.

Improvements in methodology

Undersampling, for both tree and trap types, was the main limitation of this study, primarily due to the time constraints. Consequently the treatments tested are largely underrepresented and are not reliable enough to base assumptions on. Therefore, in future, more individual trees of each type need to be sampled to ensure a good representation of the area and associated invertebrate communities between types and within the whole habitat. This will consequently be able to give results that will indicate whether or not species communities differ between tree types which were inconclusive from this study. In addition the study was conducted over a short period during late summer where traps were set for only a short length of time and when seasonality was likely have a big influence on the samples. Therefore, it is recommended that this study should be carried out for at least five years with traps remaining in the canopies for at least a week and sampling taking during each season; spring, summer, autumn, winter. This would give a more accurate representation of the invertebrate communities found within the Scottish Caledonian forest and how the assemblages change with seasons. Moreover, not enough environmental variables were measured that could be influential in explaining the species distributions and community composition. Therefore it is recommended that parameters such as light levels, humidity and wind speed, be taken within the canopy of the sample trees for the trapping duration.

Most trapping methods worked well and caught many individuals. However, the thrashing treatment was carried out on the sample trees during the same period as other trapping methods. This may have had an influence on the trapping efficiency of the other methods, as thrashing is very intrusive and may have caused considerable disturbance to the invertebrates within the tree and to the tree itself. Therefore, distributing the treatment types individually between trees should be considered so that they do not have an effect on each other. Platform-pitfall traps appeared to collect poor data in this study, whereas in previous studies they were thought to be effective methods for collecting high abundances of species (Ward et al. 2001). This may have been due to their tendency to be easily moved by wind as a few of the traps had to be adjusted back into place throughout this study. In future, these pitfalls could be attached securely to the tree with string (ideally a colour similar to the bark for camouflage) by directly accessing the canopy via a double rope technique (DRT). In addition, it is recommended that the ethylene glycol solution used in the pitfall traps is exchanged with a colourless solution, such as a clear solution of alcohol (70% ethanol), as was used for the preservation of collected invertebrates. However, there are safety issues to be considered in using alcohol in an open trap (Woodcock, 2005).

Conclusions

This study was unable to fully investigate and draw reliable conclusions about the invertebrate communities and assemblages within these Caledonian trees. However it was a preliminary investigation into testing invertebrate trapping methods within trees for future application to fragmented and regenerating areas to track changes in forest communities. Therefore, potentially using these canopy invertebrates as bio-indicators of forest health, indicating habitat deterioration or regeneration and monitoring the effects (positive or negative) of current and future management strategies. Evaluated areas may also then be used as reference sites for comparative studies of similar habitats. Further research needs to examine whether specific taxa found within these trees can be used as good indicators of habitat health. For example, the presence of predatory beetles may be used in indicating the presence of its associated prey (Humphrey et al. 1999). Also, studies on invertebrates and host-specificity may become important for future research, helping in creating a better understanding of invertebrate–plant relations and associated community level interactions.

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